Weed Technology. 2004. Volume 18:1221–1225

Symposium

Insights to Invasive Species Dynamics from Desertification Studies[1]

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Abstract: The objective of this paper is to provide insights into exotic and native invasive species dynamics using a conceptual model developed from the long history of research on native woody plant invasion into perennial grasslands in the southwestern United States. We first describe our new conceptual model that focuses on landscape characteristics (spatial configuration and connectivity) interacting with environmental drivers and biotic processes across multiple scales. We then provide support for the model using a long-term data set from southern New Mexico. Our results show that both local and spatially contagious processes can be important in generating temporal and spatial variation in native grass cover. Upland grass basal cover was related to both local (soil texture, precipitation, grazing by cattle) and spatial processes (shrub seed dispersal). Lowland grass basal cover was related to local processes associated with plant available water as well as grazing by cattle. We discuss new insights that this model has to offer for understanding, predicting, and managing exotic invasive species dynamics.

Additional index words: Chihuahuan Desert, conceptual model, landscape connectivity, landscape context.

INTRODUCTION

Woody plant invasion into perennial grasslands is a global problem in arid and semiarid regions that has been occurring for centuries in many locations (Kassas 1995; Le Houérou 1996; Reynolds 2001). In many cases, this invasion is a result of increases in local density as well as expansion of the geographic distribution of native woody plants. Numerous studies have been conducted on this ‘‘desertification process,’’ and the multiple interacting factors affecting invasion by woody plants have been identified (Archer 1994; Humphrey 1958). However, there is extremely high spatial and temporal variation in invasion dynamics such that a general consensus does not exist regarding the key factors that control different outcomes under similar conditions. Furthermore, this variation cannot be explained using current conceptual models of desertification (e.g., Ludwig et al. 1997; Reynolds et al. 1997; Schlesinger et al. 1990).

Recently, a new conceptual model was developed that focuses on landscape characteristics (spatial configuration and connectivity) interacting with environmental drivers and biotic processes across multiple scales that shows great promise in explaining and predicting this variation in woody plant invasion dynamics (Peters et al. 2004). The objective of this article is to provide insights into exotic and native invasive species dynamics and management using our conceptual model developed from the long history of research on native woody plant invasion.

CONCEPTUAL MODEL OF WOODY PLANT INVASION

Our model is hierarchically structured and includes three interacting aspects of ecological systems that affect dynamics within and among spatial units (e.g., plants, patches, landscape units): (1) variation in biotic processes and abiotic factors and the disturbance regime as well as feedbacks among these system components, (2) contagious or neighborhood processes that connect different plants, patches, and landscape units, and (3) landscape characteristics (Peters et al. 2004). Interactions among physical factors and biotic processes (plant, animal, soil) are critical to dynamics both within and among spatial units and can generate both positive and negative feedback mechanisms. Transfers of materials (water, soil, nutrients, seeds) by vectors (wind, water, animals) generate contagious processes that can occur both within and

[1] Received for publication January 7, 2004, and in revised form May 4, 2004.

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among spatial units at the same hierarchical level (e.g., patch to patch) as well as those between hierarchical levels (e.g., plant to patch and vice versa). The relative importance of transfers of materials is affected by landscape characteristics, including (1) landscape structure (size, shape, and type of spatial units), (2) spatial distribution or configuration of spatial units, and (3) the context or location and characteristics of a study area relative to its surroundings.

These landscape characteristics influence connectivity by modifying the ability of vectors to move materials horizontally. Highly connected landscapes consist of a mosaic of spatial units distributed in such a way to promote the movement of materials through spatial processes, whereas landscapes with low connectivity may have barriers or spatial configurations that restrict movement of materials. Landscape context can directly influence ecosystem dynamics: a grass patch adjacent to a stand of woody plants is more likely to be affected by the structure and dynamics of the woody plants than a similar grass patch located adjacent to a grassland.

LANDSCAPE-SCALE VARIATION IN INVASION DYNAMICS

Our new conceptual model has been instrumental in explaining temporal and spatial variation in dynamics in woody plant invasion and grass persistence. One study illustrates the usefulness of this model. At the Jornada Experimental Range in southern New Mexico (32°37′N, 106°40′W), 106, 1-m^2 permanent quadrats were established between 1915 and 1932 across a range of grassland types. Most quadrats were charted annually until 1947 and then periodically up to the present. Previous analyses of the data focused on average changes in grass cover through time (Gibbens and Beck 1987, 1988) or species-specific responses (Yao et al. unpublished data).

A recent analysis that used our new conceptual model focused on temporal and spatial variation in perennial grass basal cover for quadrats located in lowlands or uplands. We were most interested in the variation in grass basal cover for three time periods (before, during, and after the severe drought of the 1950s) that could be explained by either local (e.g., competition for soil water) or spatially contagious processes (e.g., shrub seed dispersal).

In general, our results show that the cover of grasses located in uplands was less than in lowlands (Figure 1a). Coefficient of variation for both locations was lowest in the early 1900s (1915 to 1950); variation remained low for lowland quadrats throughout the drought and post-drought periods (Figure 1b). However, variation was high during the drought for upland quadrats and remained high up to the present. In addition, only 25% of the original upland quadrats were dominated by perennial grasses in 2001, whereas 91% of the lowland quadrats were grass dominated.

Additional analyses were conducted to determine the factors explaining this spatial variation in grass cover among quadrats, particularly for uplands. Spatial databases containing information on local processes, such as plant available water (soil texture, precipitation, water redistribution) and cattle stocking rates, and contagious processes (dispersal of shrub seeds from historic shrublands) were examined in a multiple regression analysis. For upland quadrats, both local (silt content, summer precipitation, cattle grazing) and contagious processes (shrub dispersal) were important to grass cover before the drought (Table 1). During the drought, water availability as influenced by sand content was important, whereas annual stocking rate and silt content were the only significant variables after the drought. By contrast, cover in lowland quadrats was only related to growing season stocking rate before the drought and to winter precipitation after the drought; none of these variables were significant during the drought. Thus, spatial databases based only on local processes that are typically used in spatial analyses were only sufficient to explain variation in perennial grass cover in lowlands and for uplands during and after the drought. Before the drought, it was only by including contagious processes of shrub seed dispersal that variation in local grass cover in uplands was explained.

Although the regressions were significant, only 26 to 51% of the variation in upland quadrats and 15 to 40% of the variation in lowland quadrats were explained in the above analyses. Thus, additional sources of variation as a result of local and contagious processes operating at multiple scales are expected to be important to grass survival. Redistribution of water, nutrients, and seeds from upslope to downslope positions as well as between plants and bare soil interspaces can affect local grass persistence (Parsons et al. 2003; Schlesinger and Jones 1984; Wainwright et al. 2002). Redistribution of soil particles and seeds by wind can also influence shrub expansion as well as grass mortality through soil erosion and deposition (Okin and Gillette 2001). Small and large animals have effects beyond removal of biomass by grazing and seed dispersal, such as trampling and nutrient redistribution (Havstad et al. 2004; Whitford 2004). Thus, a shift in focus from explaining average conditions

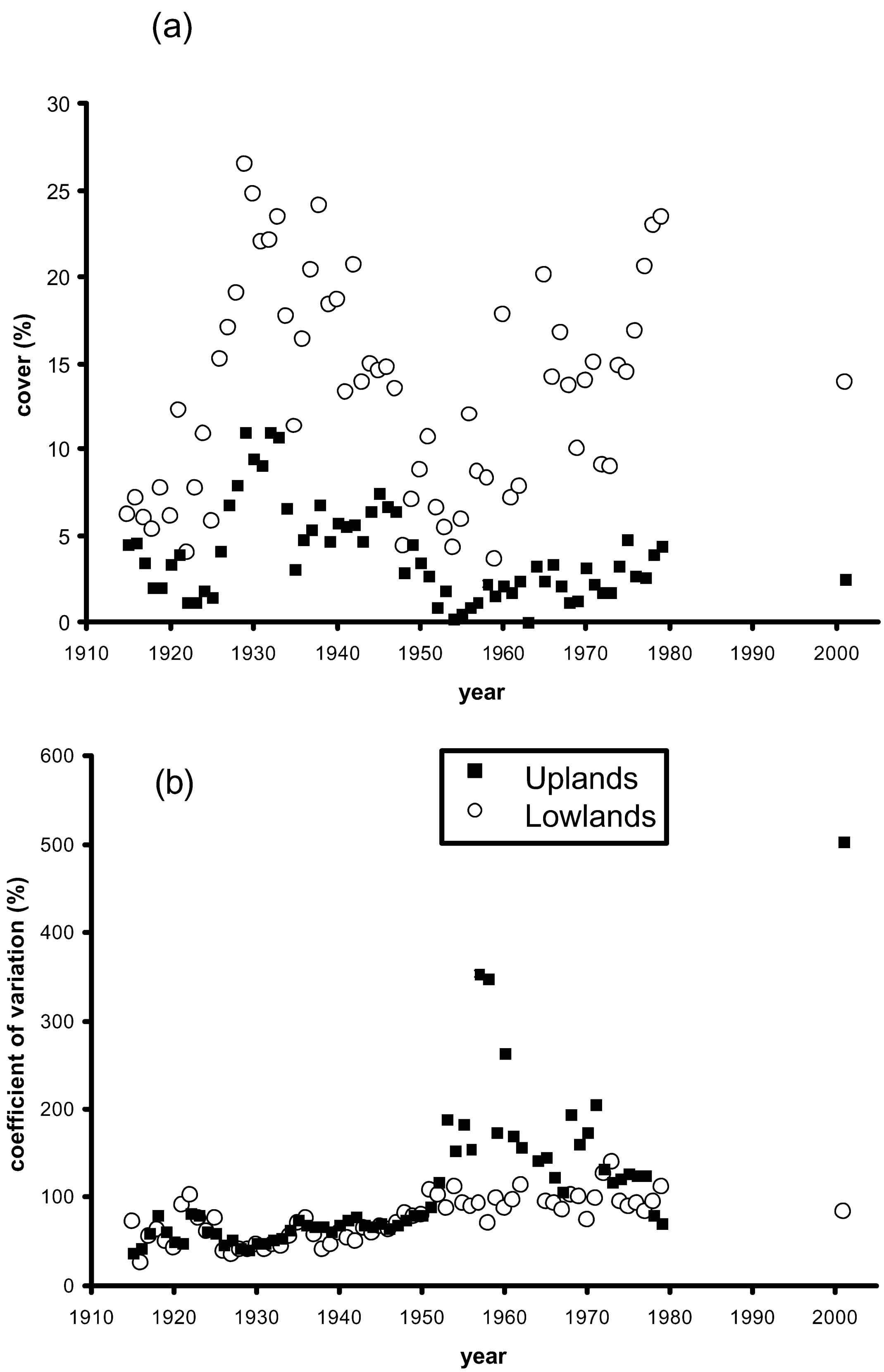

Figure 1. (a) Perennial grass cover and (b) coefficient of variation in grass cover through time for two locations (uplands, lowlands).

Table 1. Regression coefficients for perennial grass basal cover (%) in upland and lowland quadrats during each of three time periods: predrought (1915–1950), drought (1951–1956), and postdrought (1957–1979).

	Uplands			Lowlands		
	Predrought	Drought	Postdrought[a]	Predrought	Drought	Postdrought
Y intercept	−19.9	13.8	−3.3	29.9		210.4
N (no. quadrats)	61	44	40	34		15
r^2	0.38***	0.26***	0.51***	0.15*		0.40*
Local factors						
Soil texture by depth (%)						
Sand (5–20 cm)		−0.1				
Silt (5–20 cm)	0.1		0.2			
Cattle stocking rate (animal unit/ha)						
Annual	6.8		7.8			
Growing season				−166.9		
Winter precipitation (mm/November–February)						−4.3
Summer precipitation (mm/July–October)	0.1					
Landscape factors						
Distance to historic shrublands in 1928 (m)	0.001					

[a] Response variable was natural–logarithm transformed.
*** P < 0.001, ** 0.001 ≤ P < 0.01, * 0.01 ≤ P < 0.05.

or responses to explaining the variation in responses as a result of both local and contagious processes provides a more complete understanding of the system.

INSIGHTS OF NEW MODEL TO INVASIVE SPECIES DYNAMICS

The long history of research on desertification conducted globally and in the southwestern United States has led to a new view of native woody plant invasion dynamics that focuses on landscape characteristics and contagious processes interacting with local biotic processes, climate, and disturbance. Our model has improved our understanding of variation in native woody plant invasion and grass cover. The model can also provide insight into the dynamics of a broad range of types of invasive species, from herbaceous to woody and native to exotic. For example, the heterogeneous invasion patterns of many invasive species are a result of both local factors that influence competitive interactions for plant available water and contagious processes of seed dispersal (Sheley and Petroff 1999). Based on our experience, a landscape approach that encompasses ecosystem processes and vectors of redistribution across a range of spatial and temporal scales is needed to address invasive species issues. This approach also needs to include feedback mechanisms among plants, animals, and soils and the interactions between these mechanisms and landscape characteristics. Threshold behavior at multiple spatial and temporal scales and connections among scales can also be important drivers in generating variation in invasive species dynamics that can be explained with our approach (Peters et al. 2004).

Our model also has direct application to management and remediation strategies after invasion. Understanding the factors and processes allowing variation in local grass cover, despite landscape-scale woody plant invasion, may provide guidelines for experimental manipulations to increase the probability of grass recovery. For example, lowlands with persistent grass cover may be used to trigger grass recovery across a broader area (Whisenant 1999). Much of the research on invasive species has been site- and species-specific (Mack et al. 2000), with some connection to landscape ecology (With 2002). Applying a conceptual framework that focuses on variation across landscapes that includes both local and contagious processes may provide a way to connect and understand seemingly disparate results, much in the same way our model has been used in the study of native woody plant invasion into perennial grasslands.

ACKNOWLEDGMENT

This research was supported by National Science Foundation grants to New Mexico State University (DEB 00-80412, DEB 00-04526, DEB 00-87289).

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